

Elevated CO₂ Increases Wheat CER, Leaf and Tiller Development, and Shoot and Root Growth

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With 4 figures and 3 tables

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Abstract

Whole-plant responses to elevated CO₂ throughout the life cycle are needed to understand future impacts of elevated atmospheric CO₂. In this study, *Triticum aestivum* L. leaf carbon exchange rates (CER) and carbohydrates, growth, and development were examined at the tillering, booting, and grain-filling stages in growth chambers with CO₂ concentrations of 350 (ambient) or 700 (high) $\mu\text{mol mol}^{-1}$. Single-leaf CER values measured on plants grown at high CO₂ were 50% greater than those measured on plants grown at ambient CO₂ for all growth stages, with no photosynthetic acclimation observed at high CO₂. Leaves grown in high CO₂ had more starch and simple sugars at tillering and booting, and more starch at grain-filling, than those grown in ambient CO₂. CER and carbohydrate levels were positively correlated with leaf appearance rates and tillering (especially third-, fourth- and fifth-order tillers). Elevated CO₂ slightly delayed tiller appearance, but accelerated tiller development after appearance. Although high CO₂ increased leaf appearance rates, final leaf number/culm was not effected because growth stages were reached slightly sooner. Greater plant biomass was related to greater tillering. Doubling CO₂ significantly increased both shoot and root dry weight, but decreased the shoot to root ratio. High CO₂ plants had more spikes plant⁻¹ and spikelets spike⁻¹, but a similar number of fertile spikelets spike⁻¹. Elevated CO₂ resulted in greater shoot, root and spike production and quicker canopy development by increasing leaf and tiller appearance rates and phenology.

Key words: carbohydrates — CO₂ — development — phenology — photosynthesis — wheat

Abbreviations: CER, carbon exchange rate — GDD, growing degree-days — PPFD, photosynthetic photon flux density

Introduction

Projected increases in global CO₂ concentration, which is expected to double to 700 $\mu\text{mol mol}^{-1}$ in

the next century (e.g. Alcamo et al. 1996), have prompted research into the effects of elevated CO₂ on plant photosynthesis, growth and development. It is well established that the photosynthetic rate of C₃ plants is enhanced by short-term exposure to elevated CO₂. However, this enhancement is not always maintained during long-term CO₂ enrichment (e.g. Sage et al. 1989).

Photosynthetic rates and carbohydrate production are known to influence growth and development. Many studies have shown enhanced growth of plant organs and yield under high CO₂ conditions (e.g. Cure and Acock 1986, Chaudhuri et al. 1990, Hocking and Meyer 1991, Mitchell et al. 1996). A few studies have examined specific wheat developmental responses under elevated CO₂ levels, showing altered rates of leaf and spikelet primordia initiation, leaf appearance, and tiller production and abortion (e.g. Gifford 1977, Mohapatra 1990, Frank and Bauer 1996). Yet, if Arp (1991) is correct in that sink demand for photosynthates is an important feedback influencing photosynthetic rates, then altered developmental and growth rates will probably alter sink demand and the timing of sink demand for photosynthates. This interaction between whole-plant physiology and development suggests that understanding wheat responses to expected increases in CO₂ levels requires examination of whole-plant responses throughout the life cycle.

Our objectives were to determine the response of spring wheat photosynthesis, leaf carbohydrate, shoot apex development, and whole-plant growth throughout the life cycle to projected future global CO₂ concentrations. Plants were sampled at three developmental stages (tillering, booting and grain-

filling) to investigate the relationship of sink strength to photosynthesis, leaf carbohydrates, and growth.

Materials and Methods

Spring wheat (cv. Olaf) seeds were germinated on filter paper and sown in sand-filled pots. Large 14-l pots were used to minimize root binding. Water and nutrients were supplied at levels sufficient to eliminate complicating effects of water and nutrient limitations. Plants were irrigated daily with half-strength Hoagland solution (Hoagland and Arnon 1950) with supplemental $\text{NH}_4\text{-NO}_3$ (400 p.p.m. total N) and pots were flushed with water every third irrigation. Twenty pots, with one plant per pot, were placed in each of two growth chambers (Environmental Growth Chamber, Chagrin Falls, OH) with $900 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) measured at the shelf height and 60/80 % day/night relative humidity. Temperature and photoperiod were varied over the course of the experiment to approximate field conditions of the Northern Great Plains, USA; 14/8 °C day/night and 14.5-h photoperiod at the beginning of experiment and increasing weekly to 25/15 °C and 16 h at the end (about 0.7 °C and 0.1 h per weekly increase). Very slight differences in temperature occasionally occurred between the chambers, but converting results to growing degree-days (GDD) helped alleviate any potential extraneous discrepancies between treatments. One growth chamber was kept at 350–375 $\mu\text{mol mol}^{-1}$ CO_2 (ambient) and the other at 700–750 $\mu\text{mol mol}^{-1}$ CO_2 (high) at all times. The CO_2 concentration was monitored with an infrared gas analyser and pure CO_2 was automatically injected into the air circulation system when levels dropped below 350 or 700 $\mu\text{mol mol}^{-1}$.

Five plants in separate pots were observed periodically to measure shoot apex development. Each culm was identified according to the naming scheme of Klepper et al. (1982). The number of leaves on a shoot, or Haun growth stage (Haun 1973), was recorded at least weekly. The time of culm appearance, rate of leaf appearance (or phyllochron), Feekes growth stage (Large 1954), and spike development were measured for the main stem, T0, T1, T10, T11, T2 and T3 culms. Growing degree-days were calculated by Method 1 of McMaster and Wilhelm (1997):

$$\text{GDD} = [(T_{\text{max}} + T_{\text{min}})/2] - T_{\text{base}},$$

where T_{max} and T_{min} are the daily maximum and minimum temperatures, respectively, and T_{base} is the base temperature. If $(T_{\text{max}} + T_{\text{min}})/2$ is less than T_{base} , then the quantity was set equal to T_{base} . A base temperature of 0 °C was used (McMaster and Smika 1988).

Photosynthetic rate, carbohydrate accumulation and growth data were collected from five plants, in separate pots, per CO_2 treatment at tillering (Feekes growth stage 5, Large 1954, Haun \approx 5), booting (Feekes growth stage 10; Haun \approx 10 and the flag leaf), and grain-filling (Feekes growth stage 11.2), 5, 9 and 13 weeks after sowing, respec-

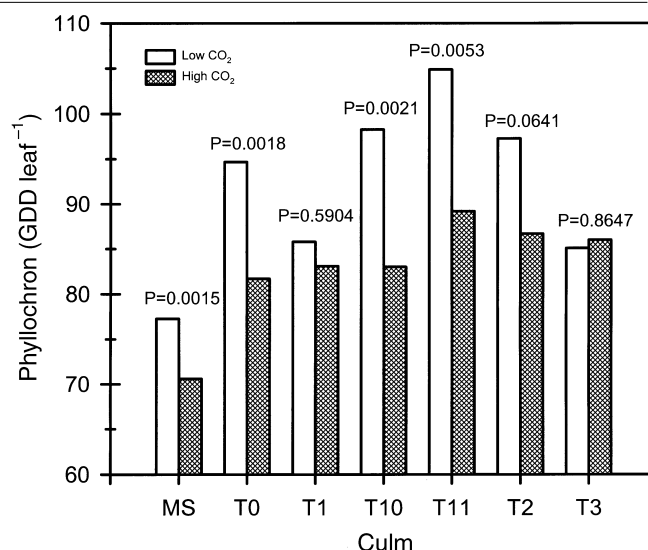


Fig. 1: Phyllochron data for specific culms. Plants were grown in either 350 or 700 $\mu\text{mol mol}^{-1}$ for the entire growth cycle

tively. Leaf CO_2 exchange rate (CER) was measured with the ADC steady-state photosynthesis system (LCA-2 with PLC-N leaf cuvette; Analytical Development Company, Hoddeson, UK), using the youngest fully expanded main stem leaf blade during tillering (measurements usually taken at the 5th leaf stage), and main stem flag leaf blades at booting and grain-filling. Both CO_2 treatments were measured using bottled air of 400 and 800 $\mu\text{mol mol}^{-1}$ CO_2 at 25 ± 1 °C. Flow rate through the cuvette was adjusted to maintain CO_2 concentration at growth conditions of 350 and 700 $\mu\text{mol mol}^{-1}$. Measurement of PPFD was $1600 \pm 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ to ensure light saturation of photosynthesis. At the same time, six 0.32-cm 2 leaf samples were collected from the midsection of a similar leaf and placed in cold 80 % ethanol for starch, sucrose, glucose and fructose analysis according to Hendrix (1993). Since the trends for each of the specific sugars were similar, only total sugar data are presented here. After CER and blade carbohydrate measurements were made, tillers were counted and plants were harvested. Roots were washed free of the sand media. Plant tissues were oven-dried at 65 °C to constant weight.

Data were analysed using SAS statistical software (SAS 1994) and are presented as means of five plants, with probabilities that the null hypothesis is true by ANOVA. Developmental data were analysed assuming repeated measurements.

Results and Discussion

Leaf appearance

Observed phyllochrons, or rate of leaf appearance (Fig. 1), in our experiment is well within that reported in the literature (McMaster et al. 1991, McMaster and Wilhelm 1995), suggesting that the

Table 1: Phenological, tiller appearance, and final leaf production results of spring wheat plants grown at 350 $\mu\text{mol mol}^{-1}$ (low) or 700 $\mu\text{mol mol}^{-1}$ (high) CO₂

Treatment	GDD to culm appearance ¹ (°C·day)	GDD to anthesis ¹ (°C·day)	GDD from culm appearance to anthesis (°C·day)	MS Haun at tiller appearance	Final Haun growth stage (no. leaves)
Main Stem					
High CO ₂	—	1094	1044	—	10.4
Low CO ₂	—	1154	1104	—	10.0
P	—	0.21	0.21	—	0.18
T1					
High CO ₂	231	1156	925	2.8	7.8
Low CO ₂	217	1193	976	2.9	8.0
P	0.07	0.06	0.04	0.19	0.62
T10					
High CO ₂	340	1212	871	4.7	7.1
Low CO ₂	322	1228	908	4.6	6.5
P	0.15	0.02	0.19	0.09	0.15
T11					
High CO ₂	404	1167	762	5.5	5.9
Low CO ₂	386	1212	823	5.4	5.8
P	0.06	0.20	0.15	0.08	0.37
T2					
High CO ₂	291	1156	864	3.8	7.1
Low CO ₂	278	1193	915	3.7	7.0
P	0.13	0.06	0.03	0.13	0.78
T3					
High CO ₂	368	1130	753	5.1	6.0
Low CO ₂	365	1160	796	5.2	5.6
P ²	0.85	0.52	0.25	0.55	0.37

¹Calculated from time of sowing. Emergence was about 50 GDD after sowing.²P is the probability that the null hypothesis is true.

growth chambers did not have any unusual effects on leaf appearance. Overall, most culms had a significantly decreased phyllochron of 10–15% in plants grown at elevated CO₂. Boone and Wall (1990) also found a difference in the phyllochron among CO₂ levels, but did not indicate the relationship. These results differ from those of Gifford (1977) and Frank and Bauer (1996) who found no effect of CO₂ on the main stem phyllochron. We do not know why the T1 and T3 culms did not show a response to CO₂, when the other culms did. There was a highly significant ($P = 0.0001$) difference in the observed phyllochron when pooling all culms within a treatment, as was also found by Boone and Wall (1990). The phyllochron tended to be positively correlated with the time of culm appearance (derived from Table 1) regardless of CO₂ level, with later-appearing culms (excluding T3) having a greater phyllochron.

Despite differences in the phyllochron among

treatments, we found no significant effect of CO₂ on the final number of leaves produced on a culm (final Haun, Table 1), although for all culms except T1, final Haun was greater for plants grown at high CO₂. Gifford (1977) also found no difference in final leaf number. Both the rate and duration of leaf appearance determine the final number of leaves on a shoot. In our experiment, the effect of elevated CO₂ was to increase the rate and decrease the duration of leaf appearance (i.e. GDD from seeding to booting), resulting in compensatory effects and no difference in final leaf number.

The phyllochron is the result of both developmental and growth processes (McMaster 1997). First cell division at the shoot apex must produce the leaf primordium, and then cell enlargement causes the leaf to emerge. Both the rate of leaf primordia initiation (or plastochron) and phyllochron are often linearly related to thermal time, but the phyllochron is more affected by other factors such

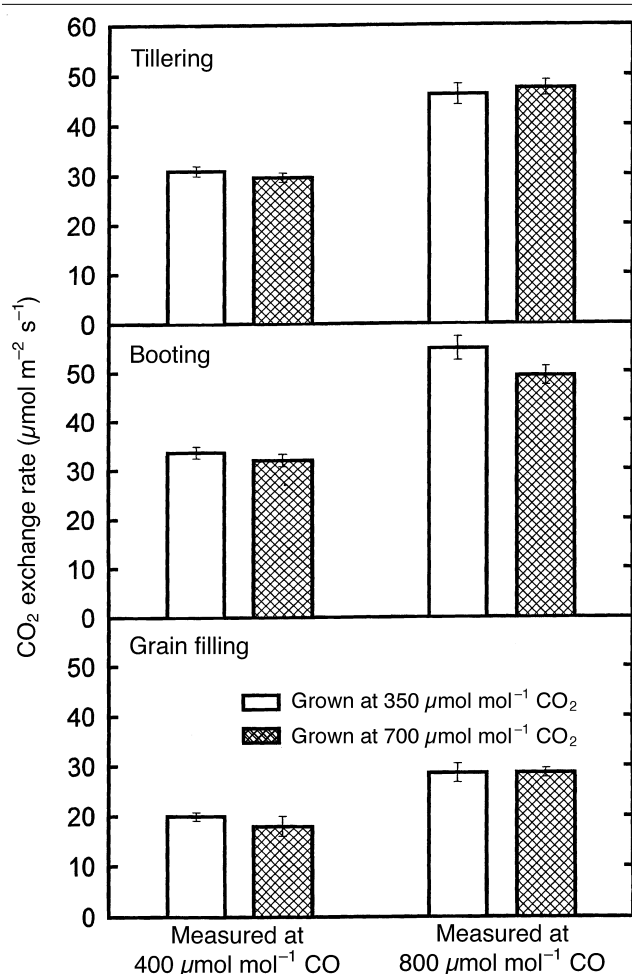


Fig. 2: Leaf blade CO₂ exchange rates of spring wheat measured at tillering (main stem Haun about 5), booting (main stem Haun about 10), and grain-filling growth stages using bottled air of 400 and 800 μmol mol⁻¹ CO₂. Plants were grown in either 350 or 700 μmol mol⁻¹ CO₂ for the entire growth cycle. Standard errors of the mean bars are included

as water, nutrients and carbohydrates than is the plastochron. Since temperature, water and nutrient conditions were the same in our experiment, and assuming an equal rate of primordia initiation, it appears that the reason for the decreased phyllochron in the high CO₂ treatment was enhanced cell growth rates. Both the CER (Fig. 2) and leaf carbohydrate (Fig. 3) data suggest that the increased cell growth rates and leaf appearance rates in plants grown at high CO₂ are probably due to increased carbohydrate availability.

CER and leaf blade carbohydrates

Regardless of growth stage or CO₂ treatment, CER was about 50 % greater when measured under elevated CO₂ conditions (Fig. 2). The least difference in

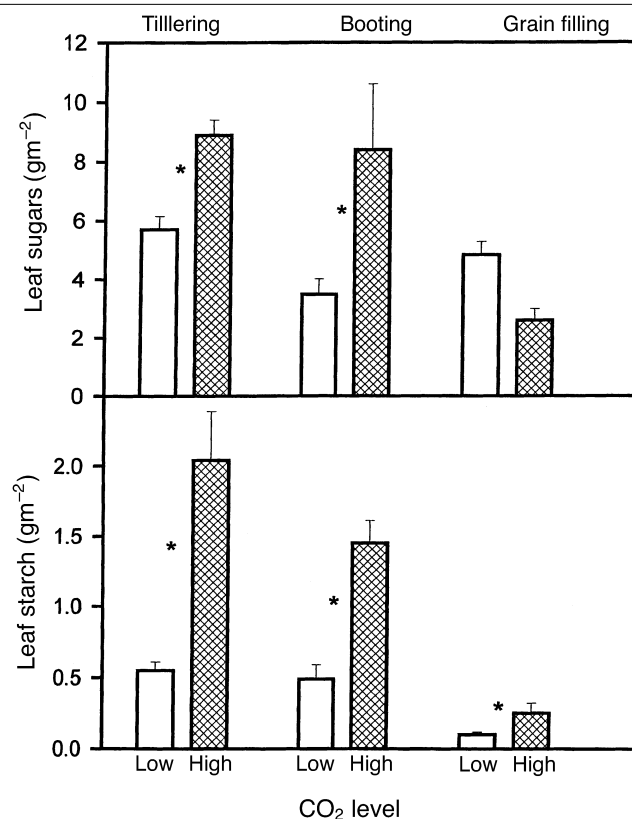


Fig. 3: Concentration of total sugars and starch in leaf blades of spring wheat at tillering (main stem Haun about 5), booting (main stem Haun about 10), and grain-filling growth stages. Plants were grown in either 350 (LOW) or 700 (HIGH) μmol mol⁻¹ CO₂ for the entire growth cycle. Standard errors of the mean bars are included. *Significant at $P \leq 0.05$

CER measured between ambient and elevated CO₂ was noted during grain-filling and the greatest difference observed during booting, with the difference for the tillering growth stage being just slightly less. Enhanced CER at elevated CO₂ has been frequently observed by others, whether exposure to elevated CO₂ was short or long term (e.g. Cure and Acock 1986, McKee and Woodward 1994, Rudorff et al. 1996).

Increased CER rates at high CO₂ were reflected in significantly greater total sugars and starch in leaf blades grown at high CO₂ at the tillering, booting and grain-filling (starch only) growth stages (Fig. 3). Surprisingly, during grain-filling there was a trend ($P = 0.099$) for more sugars in the ambient than in the high CO₂-grown plants. McKee and Woodward (1994) also found greater sucrose and starch content in flag leaves at booting in elevated CO₂ conditions. As will be discussed below, there were considerably fewer and smaller spikes on plants grown at ambient

CO₂ and perhaps the greater sugar concentration in low CO₂ leaves was due to lower sink demand by the spikes. Low concentrations of starch and sugars indicate little storage in blades at the grain-filling growth stage.

Since large pots were used in this experiment, the carbohydrate accumulation at tillering and booting is not likely to be an artifact of root binding (Arp 1991, Sage 1994). It appears that translocation of blade carbohydrates during tillering and booting does not keep pace with the greater rates of photosynthesis under elevated CO₂. Carbohydrate accumulation in blades, however, did not result in a depression of photosynthesis rates at these two developmental stages. The formation of very strong sinks at grain-filling probably eliminated the build-up of carbohydrates in high CO₂-grown flag leaves.

When measured under ambient CO₂ levels, no differences in CER were found, whether the plants were grown at either ambient or elevated CO₂ levels, although plants grown at elevated CO₂ levels tended to have lower CER (Fig. 2). Similarly, no consistent trend was found for CER rates measured at elevated CO₂ levels, regardless of the CO₂ levels the plants were grown in. Our results agree with Gifford (1977) in finding no photosynthetic acclimation in wheat grown at elevated CO₂, but differ from the findings of others who found acclimation for other species (Sage et al. 1989).

Tillering

Increased tiller production in wheat grown at elevated CO₂ has been documented by others (e.g. Gifford 1977, du Cloux et al. 1987, Hocking and Meyer 1991), although tillering strongly interacts with temperature and N levels (Frank and Bauer 1996). What has been unclear is which tillers are responding to elevated CO₂. Greater tiller production in plants grown at high CO₂ was the result of significantly more third-, fourth- and fifth-order tillers appearing (Table 2), although very high tiller numbers were observed for both treatments. It is likely that the high tiller numbers were due to plentiful water and nutrients and the fact that there was only one plant per pot. Factors known to influence apical dominance, and therefore tillering, are *rht* dwarfing genes, water, nutrients, light, temperature and carbohydrates (McMaster 1997). The first five factors were the same in the two treatments. Our results show a clear positive correlation between CER and leaf blade carbohydrate levels and tillering. Simply having plentiful water and nutrients was not sufficient to produce

as many tillers by plants grown in ambient CO₂ as in the elevated CO₂ treatment.

Greater tillering under conditions of elevated CO₂ could be a result of either greater tiller appearance, reduced abortion rates, or both. Tiller appearance stops well before booting (near the terminal spikelet stage), and the main period for tiller abortion is from jointing to anthesis (McMaster 1997). About six more tillers per plant had appeared in the high CO₂ treatment at the end of tillering stage (Fig. 4), and at booting considerably more tillers per plant were present (Table 2). Little tiller abortion was observed (data not shown), and comparison of tiller number at booting and grain-filling growth stages (Table 2) shows that little abortion occurred from booting to mid-grain-filling. Therefore, greater tillering under elevated CO₂ levels was probably the result of more tillers being produced, and in our study these were third-order and higher tillers.

Timing of tiller appearance can be viewed from several perspectives. One commonly used approach is to measure when the tiller appears after sowing, usually in days or thermal units. The cumulative growing degree-days (GDD) from sowing to the appearance of specific primary and secondary tillers was always greater for plants grown at high CO₂ levels, although the difference was significant only for T1 and T11, and then only at the 10% level (Table 1). Another approach for examining the time of tiller appearance is to base it on the main stem leaf number or Haun growth stage. In this approach, specific tillers appear during certain windows of time related to the Haun growth stage (Klepper et al. 1982, McMaster et al. 1991). Based on Klepper et al. (1982), when the main stem Haun growth stage is 3.0, 3.6, 4.8, 4.5 and 5.3, the T1, T2, T3, T10 and T11 tillers, respectively, are expected to appear, \pm about 0.5 Haun growth stage. These windows of appearance agree well with the observed data in Table 1 (2.85, 3.75, 5.15, 4.65 and 5.45, respectively, for T1, T2, T3, T10 and T11 when pooling treatments), suggesting that development under the growth chamber conditions was somewhat typical of field conditions. The mean observed Haun growth stage for the time of primary tiller appearance was not significant, regardless of CO₂ level (Table 1), but secondary tillers T10 and T11 appeared later in elevated CO₂ conditions ($d = 0.10$). Our results suggest that greater tillering at high CO₂ levels is not due to specific culms appearing sooner, rather, proportionally more third-order and higher tillers appear. Presumably this is due to greater carbohydrate availability.

Table 2: Tiller production in spring wheat plants grown at $350 \mu\text{mol mol}^{-1}$ (low) or $700 \mu\text{mol mol}^{-1}$ (high) CO_2 . Data are from the booting growth stage, except for number of spikes plant^{-1} which were measured during grain-filling. Primary tillers are produced in the axil of main stem leaves (e.g. T0, T1), secondary tillers are produced in the axil of primary tiller leaves (e.g. T10, T11), etc., according to Klepper et al. (1982)

	Tiller production						Spikes plant^{-1}
	Maximum culms plant^{-1}	1° culms plant^{-1}	2° culms plant^{-1}	3° culms plant^{-1}	4° culms plant^{-1}	5° culms plant^{-1}	
High CO_2	95	7.0	18.0	25.2	14.0	4.4	75
Low CO_2	61	6.6	17.2	17.8	7.0	1.4	46
P ¹	0.01	0.18	0.65	0.08	0.07	0.01	0.0001

¹P is the probability that the null hypothesis is true.

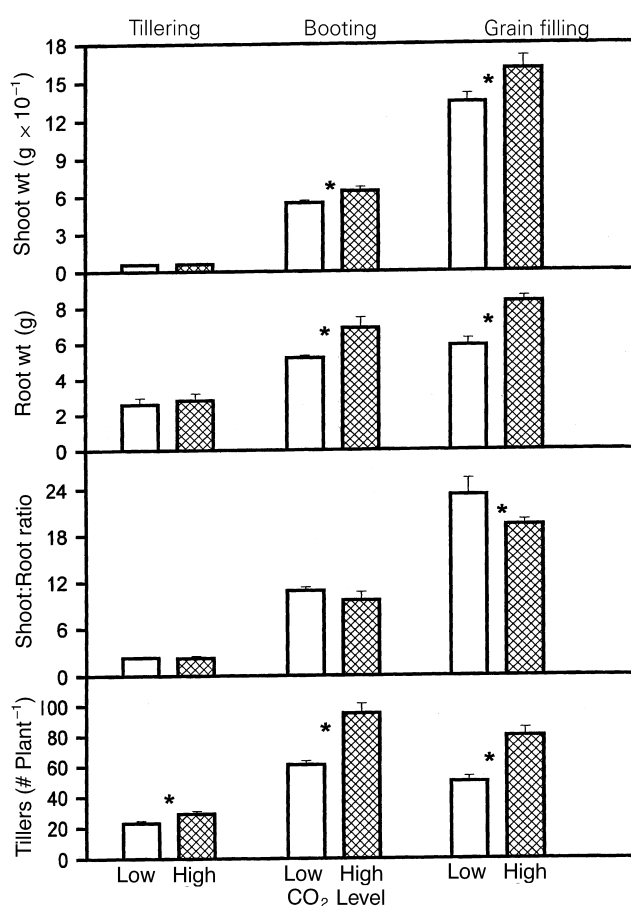


Fig. 4. Growth data of spring wheat measured at tillering (main stem Haun about 5), booting (main stem Haun about 10), and grain-filling stages. Plants were grown in either 350 (LOW) or 700 (HIGH) $\mu\text{mol mol}^{-1}$ CO_2 for the entire growth cycle. Standard errors of the mean bars are included. *Significant at $P \leq 0.05$

Phenology

Based on the phyllochron, culms were developing faster under elevated CO_2 levels, but this was poorly

correlated with culm shoot apex phenological development. Main stems of winter wheat cultivars typically reach jointing, booting, heading and anthesis about at 520, 800, 980 and 1040 GDD, respectively, after vernalization (McMaster and Smika 1988, McMaster et al. 1992). Main stems of spring wheat plants grown under ambient CO_2 levels in this experiment took about 550, 840, 910 and 1040 GDD to reach jointing, booting, heading and anthesis, respectively, suggesting that phenological development was typical of that reported under field conditions.

We observed a consistent trend (significant for T1, T10 and T2 at $\alpha = 0.10$) that culms of plants grown under high CO_2 reached anthesis slightly earlier than culms of plants grown under low CO_2 (Table 1). Mitchell et al. (1996) and Gifford (1977) reported no effect of CO_2 on phenology. When measured from sowing, culms on plants grown under high CO_2 conditions reached anthesis on average 38 GDD sooner (range was 16–60 GDD) than those culms on plants grown under ambient CO_2 conditions, and when measured from culm appearance to anthesis, the trend was stronger (mean = 48 GDD, range = 37–60 GDD). The trend for culms on CO_2 -enriched plants to reach a growth stage sooner was also observed for the growth stages of jointing (mean = 9 GDD, range = 10–29 GDD sooner), booting (mean = 9 GDD, range = –19–34 GDD sooner), and heading (mean = 26 GDD, range = –20–56 GDD sooner; data not shown). Reports differ as to whether CO_2 affects the timing of the reproductive phase; Marc and Gifford (1984) found that CO_2 enrichment advanced floral initiation, while Mohapatra (1990) found no effect of CO_2 enrichment on the timing of double ridges or terminal spikelet growth stages, which occur shortly

before jointing (McMaster 1997). Frank and Bauer (1996) found that increasing CO₂ concentration and soil N tended to delay double ridge and terminal spikelet growth stages. The smallest difference between treatments in culms reaching growth stages in our experiment was observed for the earliest growth stages (e.g. jointing and booting). Perhaps either earlier growth stages are affected less by CO₂, or the differences are not as great and therefore more difficult to detect, or the effect is additive and the small acceleration is not noted until later growth stages, or some combination of all three reasons applies.

Given our results and reports in the literature, it seems that elevated CO₂ results in tillers appearing slightly later, whether based on thermal time from sowing or main stem Haun stage. However, because these tillers have smaller phyllochrons they develop faster, and growth stages such as anthesis are reached slightly sooner. There was a very slight negative correlation between GDD to reach a growth stage and both CER and starch/sugar concentrations at the tillering and booting growth stages. This relationship agrees with the general conclusion that stress usually accelerates phenological development rates in wheat (McMaster 1997).

Normally, culms within a plant do not achieve a given growth stage at the same time (McMaster 1997). The expected pattern is that later-appearing culms reach a growth stage later than early-appearing culms, but as the plant matures, the stagger is reduced and synchrony among culms increases (Hay and Kirby 1991, McMaster 1997). This pattern was observed in our experiment, with tillers grown on plants under high CO₂ concentrations reaching anthesis on average 70 GDD later than main stems (range from 36 to 118 GDD) and tillers on plants grown at low CO₂ concentrations reaching anthesis on average 43 GDD (range from 6 to 74 GDD) later than main stems (Table 1). The trend was that plants grown at low CO₂ levels had less stagger among culms reaching anthesis than plants grown at high CO₂ levels. The GDD from culm appearance to anthesis was less the later the culm appeared after seedling emergence, so that later-appearing tillers progressed through growth stages more quickly than early-appearing tillers.

Shoot and root biomass

Greater shoot dry weight and grain yield observed in plants grown at elevated CO₂ were largely due to significantly greater tiller production at all growth

stages (Fig. 4). Differences in single leaf photosynthesis rates and leaf carbohydrates were reflected in differences in whole-plant biomass by the booting growth stage. Shoot and root dry weights were greater ($P < 0.05$) in the elevated CO₂-grown plants at booting and grain-filling, but not at tillering. It is likely that our measurements were not sufficiently precise to find differences in biomass at the tillering stage, because plants grown at elevated CO₂ had ≈ 6 more tillers than those grown at ambient CO₂ at that stage, with each tiller having slightly more leaves. Similarly, Gifford (1977) did not find improved shoot growth in spring wheat grown at high CO₂ until later in the growth cycle, and Marc and Gifford (1984) did not find significant differences for a spring wheat until 25 days after sowing, which corresponded to the single ridge growth stage. However, du Cloux et al. (1987) recorded significantly greater shoot growth in a winter wheat variety as early as 23 days after sowing.

Shoot to root ratio (Fig. 4) continually increased as maturity was approached in both treatments, as frequently reported (e.g. Sionit et al. 1981, du Cloux et al. 1987, Hocking and Meyer 1991). However, for plants grown under elevated CO₂, the shoot to root ratio increasingly became less than for those plants grown at ambient CO₂ until the difference among treatments became significant ($P < 0.05$) at grain-filling. This was due to a greater percentage increase in root dry matter compared to shoot dry matter in plants grown at elevated CO₂. Both lower and higher shoot/root ratios under high CO₂ have been reported. Rogers et al. (1996) cited 14 studies with a total of 42 treatments in addition to CO₂, and half showed an increase and half a decrease in the shoot/root ratio. Often if the limiting resource was absorbed by roots (e.g. water or macronutrients) or affected roots (e.g. soil texture) then the shoot:root ratio decreased. Water and nutrients for our study were plentiful and the shoot:root ratio increased with time, but more so in the low CO₂ treatment.

The yield component most strongly correlated with yield for wheat grown in the central Great Plains is spike number (McMaster et al. 1994). Plants grown at elevated CO₂ tillered more, resulting in significantly more spikes per plant (Table 2). Spikelets per spike is also an important yield component in wheat. Plants grown in elevated CO₂ had produced significantly more spikelets on MS, T1 and T2 spikes than those grown at ambient CO₂, but there was no difference in the number of fertile spikelets (i.e. spikelets with at least one kernel; Table 3). As noted for tillering, high CO₂ seems to

Table 3: Spike yield components. Fertile spikelets are spikelets with at least one kernel present

	MS			T1			T2		
	High CO ₂	Low CO ₂	P ¹	High CO ₂	Low CO ₂	P	High CO ₂	Low CO ₂	P
Spikelets spike ⁻¹	26.8	24.3	0.002	27.3	24.1	0.001	27.1	24.4	0.003
Fertile spikelets spike ⁻¹	18.5	18.7	0.85	19.1	18.6	0.55	19.4	18.0	0.21
Kernels spike ⁻¹	68	59.9	0.16	60.4	55.6	0.36	55.2	51.7	0.57
Kernels total spikelets ⁻¹	2.55	2.46	0.72	2.23	2.30	0.74	2.06	2.11	0.87
Kernels fertile spikelet ⁻¹	3.69	3.19	0.06	3.18	2.98	0.43	2.85	2.83	0.94

¹P is the probability that the null hypothesis is true.

have influenced apical dominance within the spike by inducing production of more spikelets, but also greater abortion of distal spikelets. The difference between total and fertile number of spikelets per spike ranged from 7.7 to 8.3 and from 5.5 to 6.4 for the high and low CO₂ treatments, respectively. For typical field conditions in the Great Plains, cultivars usually produce about 17–19 spikelets with only the basal 2 or 3 spikelets not being fertile (McMaster et al. 1994, McMaster 1997). Therefore, the range of total minus fertile spikelets per spike was high in terms of total numbers, but not when viewed as a percentage. Mohapatra (1990) found that under medium and warmer temperatures spikelet primordium initiation rates increased under higher CO₂. In contrast, Frank and Bauer (1996) found that for a spring wheat, higher total and fertile spikelets per spike at elevated CO₂ were present only at cooler temperatures, whether considering the main stem, T1 or T2 culms. Although CO₂ can be hypothesized to enhance spikelet primordia initiation through increased carbohydrate availability, which will affect total spikelets per spike, it is not known how a high CO₂ concentration would affect grain set, and thus fertile spikelets per spike. It is possible that the apical and basal spikelets, where the non-fertile spikelets were located, were not sufficiently developed to be fertilized or it is an artifact of growth chamber conditions. Although not significant, the trend was towards more kernels per spike in plants grown at high CO₂. A significant increase in kernels per spike with elevated CO₂, especially for well-watered conditions, has been reported (Chaudhuri et al. 1990). For example, Frank and Bauer (1996) and Sionit et al. (1981) found significant a CO₂ × temperature × N interaction for kernel number per spike; there was no significant difference in the number of kernels per total spikelets or fertile spikelets, but there was a

trend towards increasingly more kernels per fertile spikelet for the T2, T1 and MS culms in plants grown at elevated CO₂. Fischer and Aguilar (1976) did find more kernels per spikelet under elevated CO₂ levels. These yield component results provide insight into why yield is often greater with elevated CO₂ levels (e.g. Fischer and Aguilar 1976, Chaudhuri et al. 1990, Frank and Bauer 1996), because spikes per plant and spikelets per spike are increased by CO₂ enrichment under well-watered and high-nutrient conditions. The greater CER and leaf carbohydrate levels for plants grown under elevated CO₂ presumably provided the extra carbohydrates to support greater development and growth of these yield components.

Zusammenfassung

Erhöhtes CO₂ verstärkt CER, Blatt- und Bestockungsentwicklung sowie Sproß- und Wurzelwachstum bei Weizen

Es erscheint notwendig, die Reaktionen der Gesamtpflanze über ihren Entwicklungsverlauf zu verstehen, um Vorstellungen über die zu erwartenden Einwirkungen erhöhten atmosphärischen CO₂ zu erhalten. In dieser Untersuchung an *Triticum aestivum* L. wurden die Blattausdehnungsrate (CER) und Blattkohlenhydrate sowie Wachstum und Entwicklung in den Entwicklungsphasen Bestockung, Ährenschieben und Kornfüllung in Wachstumskammern mit CO₂-Konzentrationen von 350 (normal) oder 700 (hoch) µmol mol⁻¹ untersucht. Einzelblatt-CER an Pflanzen unter hohem CO₂ war in allen Wachstumsstadien größer als an Pflanzen unter normalen CO₂-Konzentrationen, ohne daß eine fotosynthetische Anpassung an hohes CO₂ beobachtet wurde. Blätter unter dem Einfluß hohen CO₂ hatten mehr Stärke und Einfachzucker im Stadium der Bestockung und des Ährenschiebens sowie im Stadium der Kornfüllung als unter normaler CO₂-Konzentration. CER und Kohlenhydratkonzentrationen waren positiv mit der Blattbildungsrate sowie der Bestockung (insbesondere durch

Bestockungstriebe 3, 4, und 5. Ordnung) korreliert. Erhöhtes CO₂ verzögerte leicht das Erscheinen der Bestockungstriebe, beschleunigte aber die Entwicklung der Bestockungstriebe nach ihrem Erscheinen. Obwohl hohes CO₂ die Blatterscheinungsrate beschleunigte, war die abschließende Blattanzahl/Halm nicht beeinflusst, da die Wachstumsphasen etwas früher erreicht wurden. Eine höhere Pflanzenbiomasse lag aufgrund einer stärkeren Bestockung vor. Eine Verdoppelung von CO₂ erhöhte signifikant sowohl das Sproß- als auch das Wurzel-trockengewicht, verringerte aber die Sproß-Wurzel-Relation. Pflanzen unter hohem CO₂ wiesen mehr Ähren je Pflanze und Ährchen je Ähre auf, aber eine vergleichbare Anzahl fruchtbarer Ährchen je Ähre. Erhöhtes CO₂ führte zu einer größeren Sproß-, Wurzel- und Ährenproduktion und rascherer Bestandesentwicklung bei einer Beschleunigung der Blatt- und Sproßerscheinungsraten und Phänologie.

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